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Kinship modulates the attention of naïve individuals to the mobbing behaviour of role models

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The social acquisition of life skills is essential in a wide range of species. Field experiments have demonstrated that naïve young learn particularly from their parents how to deal with predators or how to find suitable food. However, it remains unclear whether the response of young differs in a novel situation when together with related (i.e. parents) or unrelated role models. We addressed this question in a group-living bird species, the Siberian jay, *Perisoreus infaustus*, groups of which can contain both related and unrelated juveniles. Groups are formed around a breeding pair which engages in prolonged parental care, facilitating delayed dispersal of offspring for up to 5 years. About 25% of juveniles are killed by predators during their first year of life, suggesting that predator avoidance is a crucial life skill for juveniles. Exposing groups to perched predator models showed that kinship influenced how juveniles responded to the mobbing behaviour of breeders. Upon exposure to a predator model, related juveniles immediately paid attention to the behaviour of breeders and copied most of their movements. In contrast, unrelated juveniles copied the behaviour of breeders less frequently, but regularly foraged in the presence of a predator model. These results show that juveniles respond differently to parents and unrelated role models, potentially affecting the acquisition of vital life skills. Parental care creates a close social bond, predisposing juveniles to pay attention especially to novel behaviours shown by their care-givers. Furthermore, parents have a fitness benefit from facilitating the skill acquisition of their offspring. Thus, a prolonged parent-offspring association is likely to enhance skill acquisition and influence cognitive evolution across species.

Keywords: antipredator behaviour, cooperation, family living, kin group living, nepotism, parental care, predator mobbing, social learning, teaching

The acquisition of life skills is essential for most animals and much of it involves learning from others (Laland 2004; van Schaik 2010). Field studies and experiments have shown that naïve individuals learn from role models how to avoid predators, how to forage or how to choose suitable mates (Danchin et al. 2004; Freeberg 2000; Galef & Giraldeau 2001). On a proximate level, social learning ranges from social facilitation where individuals passively benefit from associating with conspecifics to learning that requires active social interactions between individuals (Laland 2004; van Schaik 2010). Consequently, social learning is widespread in species with overlapping generations and prolonged associations between parents and offspring (Drobniak et al. 2015). However, the close bond between parents and offspring makes it difficult to examine whether kinship to role models influences the behaviour of naïve individuals in a social learning context.

One of the most important life skills is predator avoidance. It involves the recognition of predators and conspecific warning calls, and the use of appropriate escape strategies (Caro 2005; Cheney & Seyfarth 1990; Griesser 2008; Griffin 2004). There is a high selective pressure for individuals to respond appropriately during the first predator encounter of their lives. Failing to do so can be lethal and in many species juveniles experience higher predation rates than adults (Caro 2005; Cheney & Seyfarth 1990; Griesser, Nystrand & Ekman 2006; Newton 1998). In species with parental care, naïve individuals can acquire or learn to refine these skills from their parents or other role models (Griffin 2004). For example, infant vervet monkeys, *Chlorocebus aethiops*, give warning calls to both predatory and nonpredatory bird species, but learn to discriminate between these species through observational conditioning from other group members (Cheney & Seyfarth 1990). Similarly, juvenile Belding's ground squirrels, *Urocitellus beldingi*, develop an appropriate response to warning calls faster when reared together with conspecifics. Also, juveniles pay more attention to warning calls from

their mother than calls from conspecifics although the reason behind this difference remains unclear (Mateo 1996; Mateo & Holmes 1997).

These observations in Belding's ground squirrels raise a crucial but largely overlooked question: does kinship influence how naïve individuals respond to role models in a novel situation? In many species, learning is vertical, meaning naïve individuals can learn from either their parents or other role models (Laland 2004). Models predict that naïve individuals should learn from any role model, independent of kinship (Rendell et al. 2010). While naïve offspring can interact with other adults in a number of species, such as in many social fish, mammal or bird species, offspring learn mainly from their parents in species with parental care. Cross-fostering experiments have demonstrated that even basic life skills, such as the acquisition of the foraging niche, can be acquired from the social parents (Slagsvold & Wiebe 2011).

The close social bond between parents and offspring may predispose offspring to learn preferentially from their parents (van Schaik 2010). Parents should be a reliable source of knowledge since they have a fitness incentive in passing on their knowledge to offspring (van Schaik, Isler & Burkart 2012). In contrast, unrelated individuals are usually not as tolerant as parents, preventing juveniles from learning socially, and experienced individuals might use unrelated juveniles as 'cannon fodder' in critical situations (Ekman 1987). Consequently, juveniles may not pay attention to the behaviour of unrelated role models. Alternatively, if the difference in knowledge between naïve individuals and role models is crucial, naïve individuals should pay attention to the behaviour of role models independent of the social relationship (Laland 2004; Rendell et al. 2010).

Here, we investigated how naïve individuals respond to related and unrelated role models in a novel situation in a social bird species, the Siberian jay, *Perisoreus infaustus*. Groups are formed through the retention of offspring with their parents beyond independence (henceforth labelled retained offspring) and/or through the immigration of unrelated nonbreeders, mostly juveniles (henceforth labelled immigrants) (Ekman, Eggers & Griesser 2002; Griesser et al. 2008). At the time of dispersal, juveniles are nutritionally independent from their parents, but during their first winter they experience a higher mortality than older individuals (assessed by following the survival of 110 radio-tagged individuals; Griesser 2013; Griesser et al. 2006). Predation is the key cause of mortality: accipiter hawks (*Accipiter gentilis, Accipiter nisus*) account for 70% of all deaths and owls account for 25% of all deaths (Griesser et al. 2006). This difference in mortality may reflect that juveniles still lack certain predator avoidance skills.

When they encounter a live perched predator or are exposed to a perched predator model, Siberian jays immediately change their behaviour by moving upwards in trees, approaching the predator by moving from tree to tree and giving a range of different mobbing calls (Griesser & Ekman 2005). Groups mob the more dangerous sparrowhawk, *A. nisus*, longer than the less dangerous Ural owl, *Strix uralensis*, and breeders in groups with retained offspring give more mobbing calls and mob longer than breeders in groups with immigrant juveniles or no juveniles (Griesser 2009; Griesser & Ekman 2005). Most mobbing calls are given by male breeders, and independent of their social rank, males swoop more often over a predator model than females.

While immigrants engage in risky behaviours more often than retained offspring (Griesser 2003; Griesser & Ekman 2005), it remains unknown whether kinship influences the response of juveniles to the predator mobbing behaviour of breeders. Earlier studies showed that birds

can learn to recognize predators from conspecifics (Curio, Ernst & Vieth 1978); thus, we predicted that juveniles would respond to the mobbing behaviour of breeders independently of their kinship. We tested this hypothesis by exposing groups to a Ural owl and a sparrowhawk model, and recording the behaviour of breeders and juvenile group members. Exposing groups to two predator models allowed us to investigate whether the risk posed by a predator and the associated difference in breeder mobbing intensity influence the behaviour of juveniles during mobbing.

<H1>Methods

This study was conducted in a population of Siberian jays that has been studied from 1989 onwards close to Arvidsjaur, Swedish Lapland (Ekman et al. 2001; Griesser et al. 2014). Here, we use field data collected between autumn 1999 and autumn 2000. Almost all birds in the study population were individually colour-ringed, aside from three individuals that were never caught. Blood (50 µl) was taken from all caught individuals for molecular sex determination (Griffiths et al. 1998). Our experiments adhere to the ASAB/ABS Guidelines for the Use of Animals in Research, the legal requirements of Sweden (where the field work was carried out) and institutional guidelines. The experiments, handling and bleeding of birds was performed under the ethics licence of Umeå djurförsöksetiska nämd (licence number A80-99 and A45-04). Ringing was performed under the licence of the Museum of Natural History, Stockholm. Our experiments involved the exposure of wild birds to models of predator species that occur at the study site. Since we used a natural setting, birds could decide how long to mob the models. We removed the models as soon as the birds stopped mobbing, and groups usually returned to the feeder at the experimental site within 30 min (Griesser & Ekman 2005).

<H2>Predator experiments

We presented perched predator models to 27 groups that included one to three naïve juveniles about 4 months of age (Table 1). For all experiments, the models were positioned 5 m from a feeder on a 1 m high pole, and concealed with a plastic cover before the jays were attracted to the feeder by whistling (Griesser & Ekman 2005). Once group members had foraged undisturbed for 15 min, the model was exposed when a randomly selected breeder and nonbreeder were together on the feeder. After the whole group had stopped mobbing and had moved more than 50 m from the experimental location, we covered the model again. For each experiment in the same group, the feeder and the model were placed in a different location near the centre of the territory.

The vocalizations and behaviour of individuals were recorded with a video camera (Griesser & Ekman 2005), and one of us (M.G.) scored all videos. For 90% of all calls it was possible to assign caller identity unambiguously; unassigned calls were excluded from the analyses (Griesser & Ekman 2005). The detailed behaviour of all group members was extracted from the videotapes using the categories listed in Table 2. We noted whether or not juveniles moved independently of a breeder (see Table 2 for the specific definitions). Moreover, we recorded all displacements (i.e. an individual is approached and forced away by another individual) among group members during the exposure to the predator models. We recorded all movements of group members from and to the feeder for 5 min before exposure to a predator model to assess whether context influenced whether or not juveniles copied movements of breeders (Table 2).

<H2>Assessment of kinship and age of juveniles

We assessed the kinship and age of juveniles using three methods. In most groups the reproductive success was monitored by locating nests and ringing all nestlings in successful broods (Eggers et al. 2006). Alternatively, juveniles were caught 1-4 weeks after they had

fledged but could still be ringed before dispersal (N = 8 broods; Ekman et al. 2002; Griesser et al. 2008). In groups in which reproduction had not been followed (N = 4 broods), juveniles were aged by the shape of the outermost tail feather (Svensson 2006) and their relatedness was assessed with the help of molecular methods (details given in Griesser et al. 2015).

<H2>Statistical analyses

The data were analysed in R 3.0.1 (R Developement Core Team 2013), using generalized linear mixed models (GLMM; glmer function in the package lme4; Bates et al. 2014) and Fisher's exact tests. We centred and scaled all the fixed terms and covariates before the statistical analyses (Schielzeth 2010). Likelihood ratio tests were used to calculate P values of all parameters (Crawley 2012). Parameter estimates and standard errors were calculated from the final models that only included significant terms (P<0.05).

We used GLMMs with Poisson error structure and log-link function to analyse the number of movements that copied movements of breeders before and during exposure to a predator model (data and R scripts are given in the Supplementary Material). We included in these models the total number of movements that juveniles made (log-transformed) as an offset variable to assess the effect of kinship on the proportion of movements juveniles were copying. We also included in these models the total number of movements made by breeders as a covariate, as it may influence the number of juvenile movements.

We used GLMMs with binomial error distribution and logit-link function to analyse whether individuals foraged during exposure (i.e. an individual landed on the feeder and foraged in the presence of the predator model), whether juveniles foraged during exposure while breeders were present (i.e. a juvenile foraged during exposure while breeders were present and mobbed the predator model), their mobbing calling behaviour (i.e. a juvenile gave mobbing calls or

not, following the categorization of Griesser (2009); including the number of mobbing calls given by breeders as a covariate), whether juveniles swooped over the predator model (including the proportion of swoops by juveniles that copied swoops of breeders, using the cbind function), and whether juveniles left the area with the predator model together with the breeders or not. Since the number of mobbing calls by juveniles was generally very low (i.e. most juveniles did not call), we used the binomial probability (juvenile called or not) in the analysis.

The following independent variables were included in all models: kinship (retained juvenile, immigrant juvenile), group size (larger groups mob more intensely; Griesser 2009), juvenile sex (males generally mob more than females; Griesser & Ekman 2005), predator model (hawk, owl; groups mob a hawk model longer than an owl model; Griesser & Ekman 2005). In addition we included group identity and juvenile identity as random terms in all models to control for the repeated sampling of some individuals and groups.

For the initial response of juveniles upon exposure to a predator model and for the foraging and aggressive behaviour of breeders during exposure to a predator model, the data points were completely separated with respect to kinship. Thus, we used Fisher's exact tests to assess the influence of kinship on these behaviours. For seven juveniles for which we had data from both experiments we only used the data point from the first one. For breeders, we assessed whether in any experiment they foraged at the feeder or displaced juveniles in the presence of the predator model.

For three reasons, the sample sizes differed within and between experiments. First, we only exposed one breeder and one nonbreeder to the model in each experiment (initial response). Second, for the behaviour upon exposure to the model, we only used the first observation for

all juveniles that were exposed to both predator models. Third, during mobbing, some nonbreeders and breeders were out of sight and, thus, we could not assess their behaviour.

<H1>Results

<H2>Natural predator encounters

Juvenile Siberian jays usually fledge at the end of May, about 4 months before our experiments. Siberian jays encountered predator species that kill jays infrequently between June and October. During the 2 years of data collection, the predator encounter rate between June and October varied between 0 and 0.0075 per territory and day for hawks (goshawks, sparrowhawks), while we never observed a large owl (hawk owl, Ural owl) during these 2 years. Of 24 territories included in this study, 22 were located in managed forests where the hawk encounter rate was even lower (0-0.0044 hawks per territory and day). Thus, most juveniles included in this study had probably never encountered a live hawk or large owl before our experiments.

<H2>Breeder response

In the absence of a predator model, group members moved to and from the feeder scatter hoarding food. Upon exposure to a perched predator model, however, group members changed their behaviour depending on rank and kinship. Upon discovering the predator model, all breeders (N = 28 breeders) sought safety in a nearby tree, from where they climbed upwards and then moved from tree to tree above the predator model, gave mobbing calls and sometimes swooped over the model (see Griesser & Ekman 2005 and above in the introduction for more details). During exposure to a predator model, breeders never visited the feeder in groups with retained offspring (N = 25 breeders), but seven of 28 breeders did so in groups without retained juveniles (Fisher's exact test: P = 0.011).

<H2>Juvenile response before breeders initiate mobbing

In three experiments with the Ural owl model, the breeder left the feeder to cash food without initiating mobbing. All three juveniles remained on the feeder and continued to forage for 5-15 s, but once a breeder returned and gave mobbing calls, all juveniles left the feeder immediately. Similarly, in three experiments with the sparrowhawk model, breeders left the feeder but did not immediately give mobbing calls or swoop over the model. Juveniles remained on the feeder to forage for 3-5 s until the breeders responded to the predator model.

<H2>Juvenile response

Before exposure to a predator model, retained and immigrant juveniles moved independently of other group members to and from the feeder (Fig. 1, Table 3). Upon exposure to a predator model, all retained juveniles ($N = 9$) followed their parents and escaped into the same tree (Fig. 1). During mobbing, retained juveniles moved frequently into the same tree or in the direction of a parent (Fig. 1, Table 3). Also, retained juveniles were more likely to give mobbing calls than immigrant juveniles (Fig. 2, Table 4), but only two of 15 retained juveniles foraged when their parents were near the predator model (Fig. 2, Table 4). However, three retained juvenile females foraged while the parents were not near the model (i.e. parents left the feeder upon exposure to the predator model without mobbing it, or parents had already stopped mobbing and had moved away; Fig. 3a, Table 4). When moving away from the model, 10 of 13 retained juveniles followed their parents (Fig. 1, Table 3). The three retained juveniles that moved away independently were all females (Fig. 3b, Table 3).

In contrast, most immigrant juveniles did not copy the behaviour of breeders. Upon exposure to the predator model, 11 of 15 immigrant juveniles escaped into a different tree than the breeder (Fisher's exact test comparing immigrant and retained juveniles: $P = 0.0006$; Fig. 1). While immigrant juveniles also remained in the vicinity of the predator model and moved

between trees, they only rarely copied movements of the breeders (Fig. 1, Table 3) and were less likely to give mobbing calls than retained juveniles (Fig. 2, Table 4). Moreover, 15 of 21 immigrant juveniles foraged in the presence of the predator model while the breeders were nearby (Fig. 2, Table 4). When moving away from the model, 13 of 19 immigrant juveniles moved away independently of the breeders (Fig. 1, Table 3).

Both retained and immigrant juveniles were less likely to give mobbing calls (Table 4) when mobbing the sparrowhawk model than when mobbing the Ural owl model. Juvenile sex and kinship influenced the feeding behaviour of juveniles in the presence of a predator model. Retained juvenile males never fed, while a few retained juvenile females and juvenile immigrants of both sexes foraged at the feeder independent of the presence of breeders (Fig. 3a).

The difference in the behaviour of retained and immigrant juveniles may reflect a difference in breeder aggression towards juveniles depending on their kinship. Five of 26 breeders displaced immigrants during mobbing ($N = 7$ displacements in total), while breeders ($N = 25$) never displaced retained juveniles during mobbing (Fisher's exact test: $P = 0.05$).

<H2>Discussion

Our observations suggest that juvenile Siberian jays rarely encounter their main predators during their first summer of life. Accordingly, we found that all juveniles continued to forage when they were exposed to a predator model without breeders. Whenever breeders initiated mobbing of the models, however, juveniles stopped foraging and joined the mobbing, but the behaviour of juveniles was influenced by their kinship to the role model. Retained juveniles copied many of the movements and behaviours of their parents during mobbing, while immigrant juveniles moved more independently of breeders during mobbing, and exposed

themselves more often to risks by foraging near a predator model. These findings suggest that retained and immigrant juveniles respond differently in a novel situation that provides an opportunity to acquire life skills. This difference is rather remarkable given that social learning is a widespread mechanism to acquire new skills (Freeberg 2000; Galef & Giraldeau 2001; Hoppitt & Laland 2008; Rendell et al. 2010). Thus, naïve individuals should take advantage of social learning opportunities independent of the kin relationship to the role model, but our experiments show that this is not the case.

<H2>Why do retained and immigrant juvenile responses differ?

The difference in the response of retained and immigrant juveniles could reflect phenotypic differences between them (Riebel et al. 2012) i.e. in body condition, body size, cognitive abilities or energetic trade-offs), social tolerance of the role models (van Schaik 2010), kin-selected benefits (Hamilton 1964) or an attention bias of offspring.

Individuals of lower phenotypic quality have been shown to have a reduced ability to copy the behaviour of role models (Riebel et al. 2012). Within broods, retained juveniles are socially dominant over their siblings that disperse after independence and become immigrant juveniles (Ekman et al. 2002). Yet, retained and immigrant juveniles do not differ in their body size (linear model: wing length: kinship estimate±SE=0.27±0.56, $P = 0.63$; tarsus length: kinship estimate±SE=-0.03±0.18, $P = 0.86$), but immigrant juveniles have a higher feather quality than retained juveniles (Griesser et al. 2006). This difference probably reflects that most forests in the study site are heavily managed (Griesser et al. 2007), leading to low-quality offspring (Eggers, Griesser & Ekman 2005) compared with offspring that are born in better quality habitat and immigrate into the study site. We did not assess the cognitive abilities of retained and immigrant juveniles in this study. However, dominant retained and immigrant

juveniles do not differ in the time they require to learn a novel foraging task independent of breeders (Wroblewski 2015).

Earlier studies showed that immigrants more often forage further from cover than retained offspring (Nystrand 2007), and start foraging without scanning for predators (Griesser 2003). Accordingly, immigrant juveniles could also take more risks during mobbing than retained juveniles. However, both retained and immigrant juveniles mobbed the predator models, but immigrant juveniles did so more independently of the breeders. This difference could reflect that breeders display more aggression towards immigrants than retained offspring. When foraging at a feeder in the absence of predator models, breeders displace immigrants on average 13 times/h (Griesser et al. 2015), but we observed only seven displacements during exposure to the models (i.e. 1.7 displacements/h; involving five immigrant juveniles). Thus, most breeders were not constraining the mobbing behaviour of immigrant juveniles. Rather, breeders can be very tolerant to opposite-sex immigrants since they can replace their current mate if it dies (Ekman & Sklepkovych 1994). Yet, we only found an effect of sex on the behaviour of retained juveniles (Fig 3, Tables 3, 4), which may reflect that male juveniles frequently displace their sisters. In the absence of predator models, immigrants usually move with other group members as a cohesive unit (Griesser et al. 2008; Griesser et al. 2006) and join other group members on feeders (Griesser 2003).

It seems unlikely that retained juveniles mob more intensely due to kin-selected benefits. While retained juveniles have close relatives in their group (siblings, parents), they do not behave nepotistically towards their siblings or parents. Dominant siblings are aggressive towards subordinate siblings (Ekman et al. 2002), and retained offspring do not engage in alloparental brood care even though they can stay up to 5 years on the parental territory (Ekman, Sklepkovych & Tegelström 1994). Also, they do not increase their vigilance rate

when feeding together with parents (Griesser 2003), or hardly ever give warning calls for a parent during attacks (1 out of 20 experiments; see Griesser & Ekman 2004).

<H2>Parental care and social learning

In most species with parental care, until nutritional independence juveniles stay close to their parents, which provide food to their offspring either through nursing, feeding them directly or, in precocial species, by guiding them to food (Allen & Clarke 2005). Thus, offspring are selected to pay attention to the behaviour of their parents, and follow their parents or other care-givers with interest, paying attention particularly to novel situations (Jaeggi, Van Noordwijk & Van Schaik 2008; Schuppli, Isler & van Schaik 2012). As a consequence, in a large number of species offspring acquire from their parents many life skills (Galef & Laland 2005; Hollen & Radford 2009), such as food preferences (van de Waal et al. 2010), foraging strategies or the foraging niche (Slagsvold & Wiebe 2011). Moreover, parents have a direct fitness incentive to facilitate skills acquisition by their offspring and improve their survival (Griesser et al. 2006). In contrast, breeders could use immigrant juveniles as 'cannon fodder' during predator attacks, increasing their own survival (Ekman 1987). Thus, immigrant juveniles might be better off by mobbing the models more independently of the breeders.

<H2>Social learning and social complexity

Recent theory suggests that social complexity may fuel the evolution of complex social behaviours, such as visual displays or vocal communication (Freeberg 2006; Freeberg, Dunbar & Ord 2012; Freeberg & Krams 2015). In Siberian jays, group composition varies due to the numbers of both nonbreeders (range 0 - 5) and kin (retained offspring, immigrants). This complex social setting may require individuals to have complex communication abilities (Freeberg 2006). Supporting this idea, our results show that juveniles respond differently to the mobbing behaviour of breeders depending on their kinship. Moreover, earlier studies

showed that breeders adjust their mobbing behaviour according to predator type, group size and group composition (Griesser 2008, 2009). Thus, having both retained and immigrant juveniles increases the complexity of social interactions within a group, which may facilitate the evolution of a large vocal repertoire (Griesser 2008, 2009).

<H2>Conclusions

Previous studies highlighted the importance of parents as role models for social learning, yet did not assess the response of naïve individuals to learning opportunities provided by role models of varying kinship (but see Mateo & Holmes 1997). Our findings show that kinship influences the behaviour of naïve individuals in a situation that may provide a social learning opportunity, thereby influencing downstream fitness. Retained juveniles have a higher survival rate during their first winter than immigrant juveniles (Griesser et al. 2006), acquire breeding openings of higher quality (Ekman et al. 2001) and leave more offspring during their lifetime (Ekman & Griesser 2016). It remains unclear whether this is an effect of parental protection (Griesser 2013), or whether retained offspring are both provided with more social learning opportunities (Griesser 2008, 2009; Griesser & Ekman 2004, 2005) and take better advantage of them (as shown here).

A broader implication of these findings is that kinship may influence how new skills spread within a population (Rendell et al. 2010). In species that only rely on vertical social learning, new skills mainly spread from parent to their offspring. However, in species that also acquire new skills horizontally through peer learning, new skills can spread more quickly (Claidière et al. 2013; O'Mara & Hickey 2012), such as the famous food-washing behaviour of Japanese macaques, *Macaca fuscata* (Kawai 1965). Moreover, the social setting that promotes social skill learning has been suggested to facilitate the cognitive abilities of species (van Schaik et al. 2012). Thus, prolonged parent-offspring associations (Drobniak et al. 2015) may provide

offspring with both more learning opportunities and the cognitive abilities to do so, allowing offspring to acquire ample life skills from their parents.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi

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Table 1

Number of juveniles and groups exposed to a sparrowhawk and a Ural owl model

	Number exposed to		Total number juveniles/groups
	Sparrowhawk	Ural owl	
Retained juveniles	10	10	15
Immigrant juveniles	10	18	22
Groups	16	22	27

Twelve juveniles were exposed to both predator models and groups included one to three juveniles.

Table 2

Behaviours shown before and during mobbing, and the definition of whether these behaviours depended on the behaviour of the breeders or not

Behaviour	Definition	Behaviour dependent on breeder behaviour	Behaviour independent of breeder behaviour
Movements before exposure	Arrive or depart from a feeder to forage or scatter-hoard food	<3 s of a breeder	>3 s of a breeder
Escape behaviour upon exposure	Escape to a nearby tree and seek cover	Escape into same tree as a breeder	Escape into different tree from a breeder
Movements during exposure	Move from tree to tree	Move in direction of or in same tree as a breeder	Move in a different direction, not approaching a breeder
Swoop	Pass within 2 m of predator model	Swoop after, join a breeder	Swoop independent of, not joining breeder
Leaving	Moving at least 50 m from model	Leave together with or follow a breeder	Leave before a breeder, or in a different direction

For movements before exposure we used 3 s as a threshold to differentiate between dependent and independent moves, given that within this time individuals move out of sight of individuals on the feeder.

Table 3

Generalized linear mixed models assessing the proportion of dependent movements of juvenile Siberian jays before and during exposure to a predator model and when leaving

Model	Variable	*df*	χ^2	*P*	Effect	SE
Proportion of dependent movements before mobbing						
Full model	Kinship	1	0	1		
	Sex	1	3.38	0.07		
	Kinship*sex	1	0	1		
	Group size	1	0.4	0.53		
	Number of breeders	1	2.38	0.12		
Proportion of dependent movements during mobbing						
Full model	Kinship	1	9.14	0.003		
	Sex	1	1.25	0.26		
	Kinship*sex	1	1.16	0.28		
	Group size	1	0.6	0.44		
	Predator species	1	2.62	0.11		
	Number of breeders	1	4.88	0.027		
Minimal model	Intercept				-0.85	0.12
	Kinship	Retained>immigrant			0.41	0.12
	Number of breeder movements				-0.3	0.14
Leaving together with breeders						
Full model	Kinship	1	6.83	0.009		
	Sex	1	0.46	0.5		
	Kinship*sex	1	6.85	0.009		
	Group size	1	0.59	0.44		
	Predator species	1	7.47	0.006		
Minimal model	Intercept				-0.64	0.53
	Kinship	Retained>immigrant			-1.26	0.62
	Kinship*Sex				-1.34	0.67
	Predator species	Hawk>owl			-1.46	0.65

All models include kinship, juvenile sex, predator species and group size as fixed terms and individual and group identity as random terms. Movements of juveniles before and during exposure included the total number of movements by breeders as a fixed term to control for the influence of number of breeder movements. Reference level of the categorical variables: kinship=immigrant juvenile; sex=female; predator species=Ural owl.

Table 4

Generalized linear mixed models assessing the mobbing behaviour of juvenile Siberian jays during exposure to a predator model

Model	Variable	*df*	χ^2	*P*	Effect	SE
Mobbing calls						
Full model	Kinship	1	8.05	0.005		
	Sex	1	1.17	0.28		
	Kinship*sex	1	0.32	0.57		
	Group size	1	2.97	0.09		
	Predator species	1	20.17	0.00001		
	Number of breeder calls	1	0.06	0.8		
Minimal model	Intercept				1.42	0.73
	Kinship	Retained>immigrant			1.9	0.86
	Predator species	Owl>hawk			-2.33	0.8
Swoop over model						
Full model	Kinship	1	0.6	0.44		
	Sex	1	0.25	0.62		
	Kinship*sex	1	0	1		
	Group size	1	0.23	0.63		
	Predator species	1	0.14	0.71		
Foraging in presence of model and breeder						
Full model	Kinship	1	8.96	0.003		
	Sex	1	4.79	0.029		
	Kinship*sex	1	1.79	0.18		
	Group size	1	0.69	0.41		
	Predator species	1	0.4	0.53		
Minimal model	Intercept				-0.91	0.46
	Kinship	Immigrant>retained			-1.15	0.48
	Sex	Female>male			-0.65	0.42
Forage in presence of model						
	Kinship	1	3.33	0.068		
	Sex	1	8.81	0.003		
	Kinship*sex	1	4.84	0.028		
	Group size	1	0.01	0.92		
	Predator species	1	2.53	0.11		
Minimal model	Intercept				-0.36	0.5
	Sex	Female>male			-1.12	0.49
	Kinship*sex				-0.77	0.51

All models include kinship, juvenile sex, predator species and group size as fixed terms and individual and group identity as random terms. Mobbing call model included the total

number of mobbing calls by breeders as a fixed term; swooping model included the total number of swoops by breeders as a fixed term to control for breeder mobbing intensity. Reference level of the categorical variables: kinship=immigrant juvenile; sex=female; predator species=Ural owl.

Figure 1. Proportion of dependent movements of retained and immigrant juvenile Siberian jays before and during exposure to a predator model. Definitions of dependent and independent movements are given in Table 2. Error bars signify SE; error bars are not shown for behaviours with only one measurement per individual (upon exposure, when leaving). ***P*<0.01; ****P*<0.005.

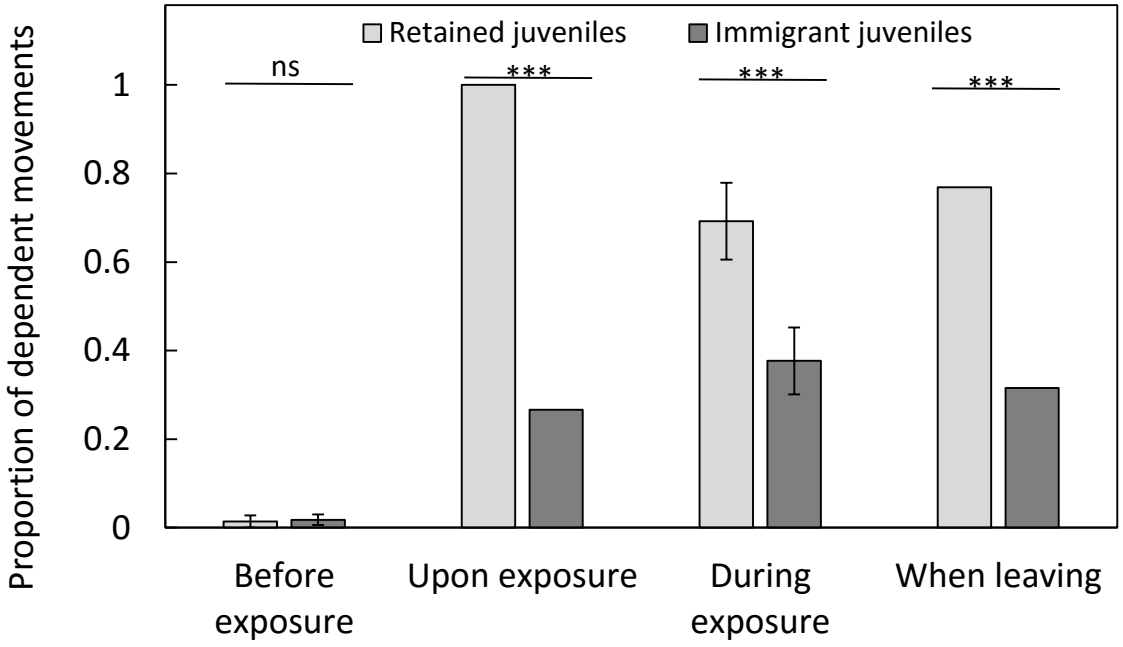

Figure 2. Mobbing behaviours and foraging behaviour of retained and immigrant juvenile Siberian jays during exposure to a predator model. Only one data point per experiment and individual. *P<0.05; **P<0.005.

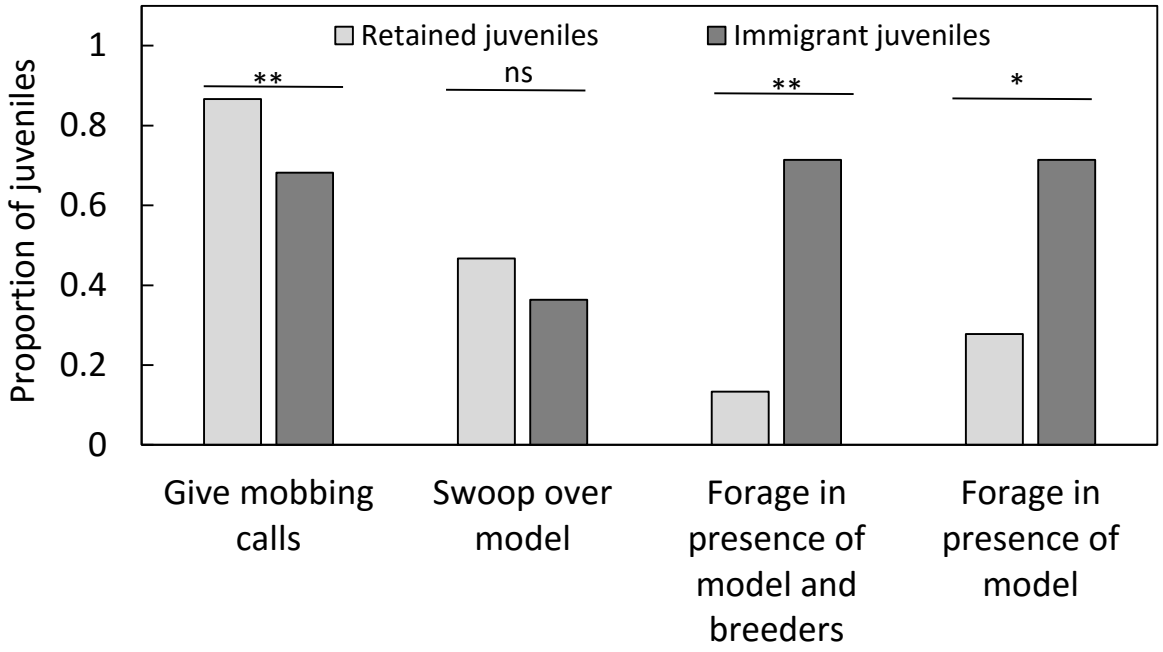

Figure 3. Differences between female and male juveniles (a) when foraging in the presence of a predator model, independent of the presence of breeders and (b) when leaving after finishing mobbing.